Natural variability or anthropogenically-induced variation? Insights from 15 years of multidisciplinary observations at the arctic marine LTER site HAUSGARTEN

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ABSTRACT

Time-series studies of arctic marine ecosystems are rare. This is not surprising since polar regions are largely only accessible by means of expensive modern infrastructure and instrumentation. In 1999, the Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung (AWI) established the LTER (Long-Term Ecological Research) observatory HAUSGARTEN crossing the Fram Strait at about 79°N. Multidisciplinary investigations covering all parts of the open-ocean ecosystem are carried out at a total of 21 permanent sampling sites in water depths ranging between 250 and 5,500 m. From the outset, repeated sampling in the water column and at the deep seafloor during regular expeditions in summer months was complemented by continuous year-round sampling and sensing using autonomous instruments in anchored devices (i.e., moorings and free-falling systems). The central HAUSGARTEN station at 2,500 m water depth in the eastern Fram Strait serves as an experimental area for unique biological *in situ* experiments at the seafloor, simulating various scenarios in changing environmental settings. Long-term ecological research at the HAUSGARTEN observatory revealed a number of interesting temporal trends in numerous biological variables from the pelagic system to the deep seafloor. Contrary to common intuition, the entire ecosystem responded exceptionally fast to environmental changes in the upper water column. Major variations were associated with a warm water anomaly evident in surface waters in eastern parts of the Fram Strait between 2005 and 2008. However, even after 15 years of intense time-series work at HAUSGARTEN, we cannot yet predict with complete certainty whether these trends indicate lasting alterations due to anthropologically-induced global environmental changes of the system, or whether they reflect natural variability on multiyear time-scales, for example, in relation to decadal oscillatory atmospheric processes.

1. Introduction

While always fluctuating, the global climate is presently experiencing a period of constantly increasing temperatures, with a warming trend amplified in the Arctic (Hassol, 2004). Results of large-scale simulations of the Earth's future climate by several global climate models predict a continuous increase in air and water temperatures, also leading to further reduction in ice-cover (IPCC, 2013). Since the 1950s, sea ice retreat in the Arctic Ocean has been relatively modest at rates of 3-4% per decade (Parkinson et al., 1999). However, since the late 1990s, annual-averaged shrinking rates accelerated to 10.7% per decade (Comiso et al., 2008), whilst the summer sea ice extent has shrunk even more rapidly. According to the US National Snow and Ice Data Center (NSIDC), arctic sea ice during the 2012 melt season has reached its lowest extent since satellites began measuring sea-ice in 1979, with 44% ice coverage below the 1981-2010 average, and 16% ice coverage below the previous minimum extent in 2007.

Moreover, according to the results from large-scale surveys carried out by US submarines equipped with upward looking sonar and ICESat satellite observations, there has been a significant thinning of the sea-ice by approximately 50% since the late 1950s (Kwok and Rothrock, 2009). Laxon et al. (2013) compared satellite and model-derived sea-ice volume data between the years 2003-2008 and 2010-2012, and found that sea-ice volume declined by 36.2% at the end of summer, and by 9.1% at the end of winter. In its recent report, the Intergovernmental Panel on Climate Change (IPCC) prophesied that the Arctic could become ice-free in the second half of this century, while Wang and Overland (2012) argued that this scenario might even take place much earlier, with predictions as early as the end of the arctic summer 2040. Greenhouse gases emitted through human activities and the resulting increase in global mean temperatures are most likely the underlying cause of the sea-ice decline, although it is recognized that the current sea-ice decline most likely resulted from a complex

interaction between natural and anthropogenic causes and variations in climate change, acting on different time scales (Drinkwater et al., 2014).

The shift from an ice-covered and cold ocean to an ice-free and warmer ocean will have severe impacts on the polar marine ecosystem and its functioning (e.g., Wassmann et al., 2011). Thinner ice may permit better growth of ice algae, but earlier and faster spring melting may reduce their growing season (Arrigo, 2013). Locally, thinner ice floes with a multitude of melt ponds allow enhanced light transmission and may increase phytoplankton growth beneath the ice (Arrigo et al., 2012; Nicolaus et al., 2012). The timing and location of pelagic primary production will generally be altered (Kahru et al., 2010). Ice-edge phytoplankton blooms will be displaced progressively northwards (Maslanik et al., 2011). Whether sea-ice retreat generally leads to an increase in primary productivity is under debate (Arrigo et al., 2008; Tremblay and Gagnon, 2009; Wassmann et al., 2010). In fact, biogeochemical models predict no or even negative changes in productivity and export flux in the Barents Sea and the Fram Strait (Forest et al., 2010; Slagstad et al., 2011).

Altered algal abundance and composition will affect zooplankton community structure (Caron and Hutchins, 2013) and subsequently the flux of particulate organic matter to the seafloor (Wohlers et al., 2009), where the changing quantity and quality of this matter will impact benthic communities (Kortsch et al., 2012; Jones et al., 2013). Changes in the predominance of certain trophic pathways will have cascading effects propagating through the entire marine community.

Generally, arctic marine organisms will be compromised by temperature regimes approaching the limits of their thermal capacity (Burrows et al., 2011, 2014). As a consequence, warmer waters in the Arctic will allow a northward expansion of sub-arctic and boreal species (Hirche and Kosobokova, 2007; Poloczanska et al., 2013). Besides water temperature increase, expanding ocean acidification will pose another threat to pelagic and

benthic life in the Arctic Ocean (e.g., Bates et al., 2009; Lischka and Riebesell, 2012; AMAP, 2013).

To detect and track the impact of large-scale environmental changes on the marine ecosystem in the transition zone between the northern North Atlantic and the central Arctic Ocean, the Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung (AWI) established the LTER (Long-Term Ecological Research) observatory HAUSGARTEN in the Fram Strait between NE Greenland and the Svalbard archipelago (Soltwedel et al., 2005). Since 1999, repeated sampling in the water column and at the seafloor during yearly expeditions in summer months was complemented by continuous year-round sampling and sensing using autonomous instruments on anchored devices. The central HAUSGARTEN station at about 79°N, 04°E in the eastern Fram Strait (~2,500 m water depth) serves as an experimental area for unique biological experiments at the deep seafloor, simulating various scenarios in changing environmental settings (Premke et al., 2006; Gallucci et al., 2008; Kanzog et al., 2009; Guilini et al., 2011; Soltwedel et al., 2013).

Time-series studies at the HAUSGARTEN observatory provide insights into processes and dynamics within an arctic marine ecosystem and act as a baseline for further investigations of ongoing changes in the Fram Strait. Long-term observations at HAUSGARTEN will significantly contribute to the global community's efforts to understand variations in ecosystem structure and functioning on seasonal to decadal time-scales in an overall warming Arctic and will allow for improved future predictions under different climate scenarios.

2. Site description

The LTER observatory HAUSGARTEN is located in a region which is influenced by the highly productive Marginal Ice Zone (MIZ) in the Fram Strait. Currently, HAUSGARTEN constitutes a network of 21 permanent sampling sites, the majority of which are located along

a bathymetric transect between ~250 m and ~5,500 m water depth at about 79°N from the Kongsfjorden (Svalbard) in the east, along the Vestnesa Ridge towards the Molloy Hole (i.e., the deepest known depression in the Arctic Ocean) and across the Greenland continental margin (stations in the western Fram Strait were newly established in 2014). Three sampling sites close to the ice edge between 79°30'N and 80°00'N in the north-eastern Fram Strait and a supplementary site in a permanently ice-free area at 78°30'N in the eastern part of the strait complete the network (Fig. 1).

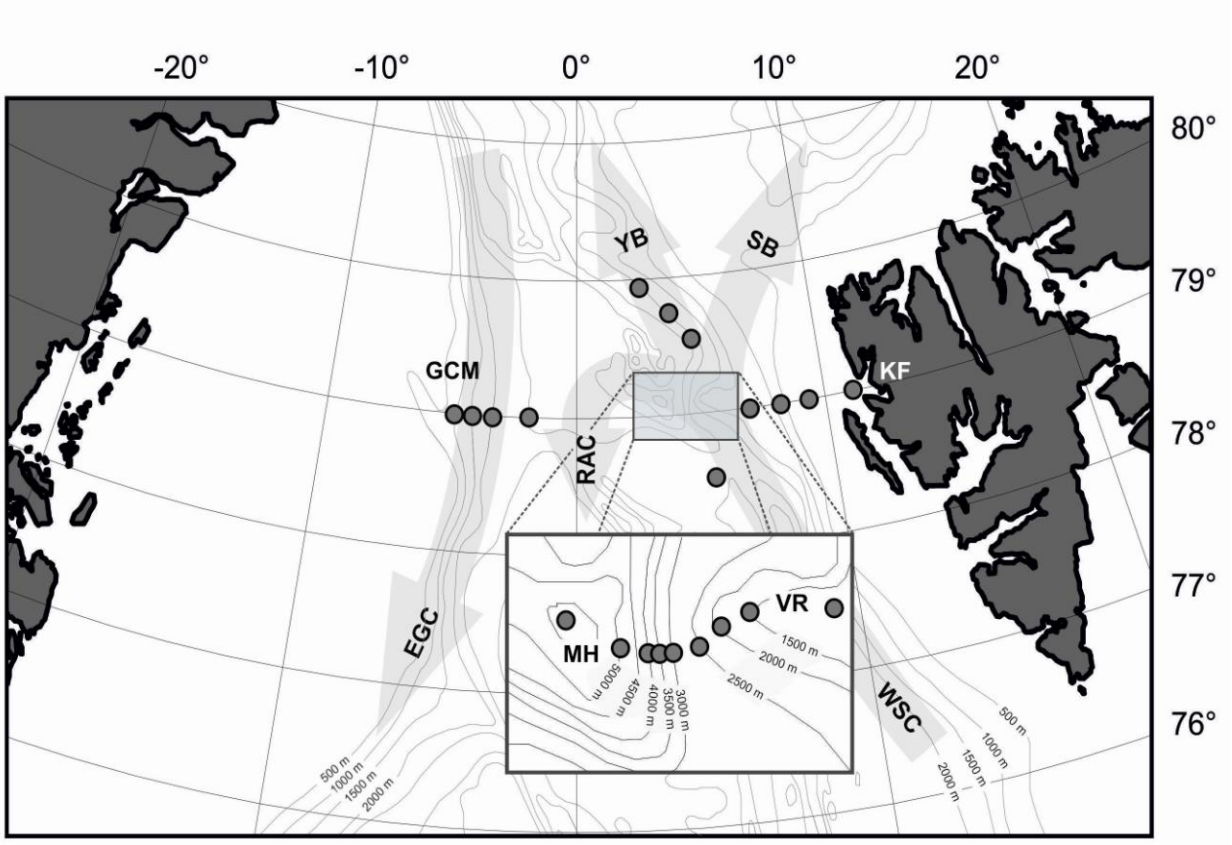

Fig. 1. Sampling sites (●) of the LTER observatory HAUSGARTEN, geographic features, and major currents in the Fram Strait (KF: Kongsfjorden; VR: Vestnesa Ridge; MH: Molloy Hole; GCM: Greenland Continental Margin; WSC: West Spitsbergen Current; EGC: Eastern Greenland Current; RAC: Return Atlantic Current; YB: Yermak Branch, and SB: Svalbard Branch of the WSC).

The Fram Strait is the only deep water connection between the Nordic Seas and the central Arctic Ocean with a sill depth of ca. 2,600 m. The hydrography in the eastern part of the strait is characterized by the inflow of relatively warm and nutrient-rich Atlantic Water (AW) into the central Arctic Ocean (Beszczynska-Möller et al., 2012). Cooler and less-saline Polar Water exits the central Arctic Ocean as the Eastern Greenland Current (EGC) in the western part of the Fram Strait (de Steur et al., 2009), separated by a frontal system (East Greenland Polar Front) from the water masses in the eastern part of the Fram Strait (Paquette et al., 2012). Hydrographic patterns in the strait result in a variable sea-ice cover, with predominantly ice-covered areas in the west, permanently ice-free areas in the south-east, and seasonally-varying ice conditions in the central and north-eastern parts. Anomalies in summer sea-ice coverage from a 30-year reference period (1981-2000) in the greater Fram Strait since the establishment of HAUSGARTEN observatory in 1999 are shown in Figure 2. Strong positive values (more sea ice compared to the long-term mean) were found in 2003, 2008, and 2009, whereas negative values (less ice compared to the long-term mean) occurred in 2001 and 2002, in 2004 through 2006, and in 2010; all other years showed intermediate values for the ice coverage at the observatory. In this way, the data showed no clear temporal trend in sea-ice coverage for the HAUSGARTEN area during the last 15 years; however, a time-series constructed from *in situ* measurements by Renner et al. (2014) exhibited a constant thinning of the sea ice by over 50% at the end of the melt season between 2003 and 2012.

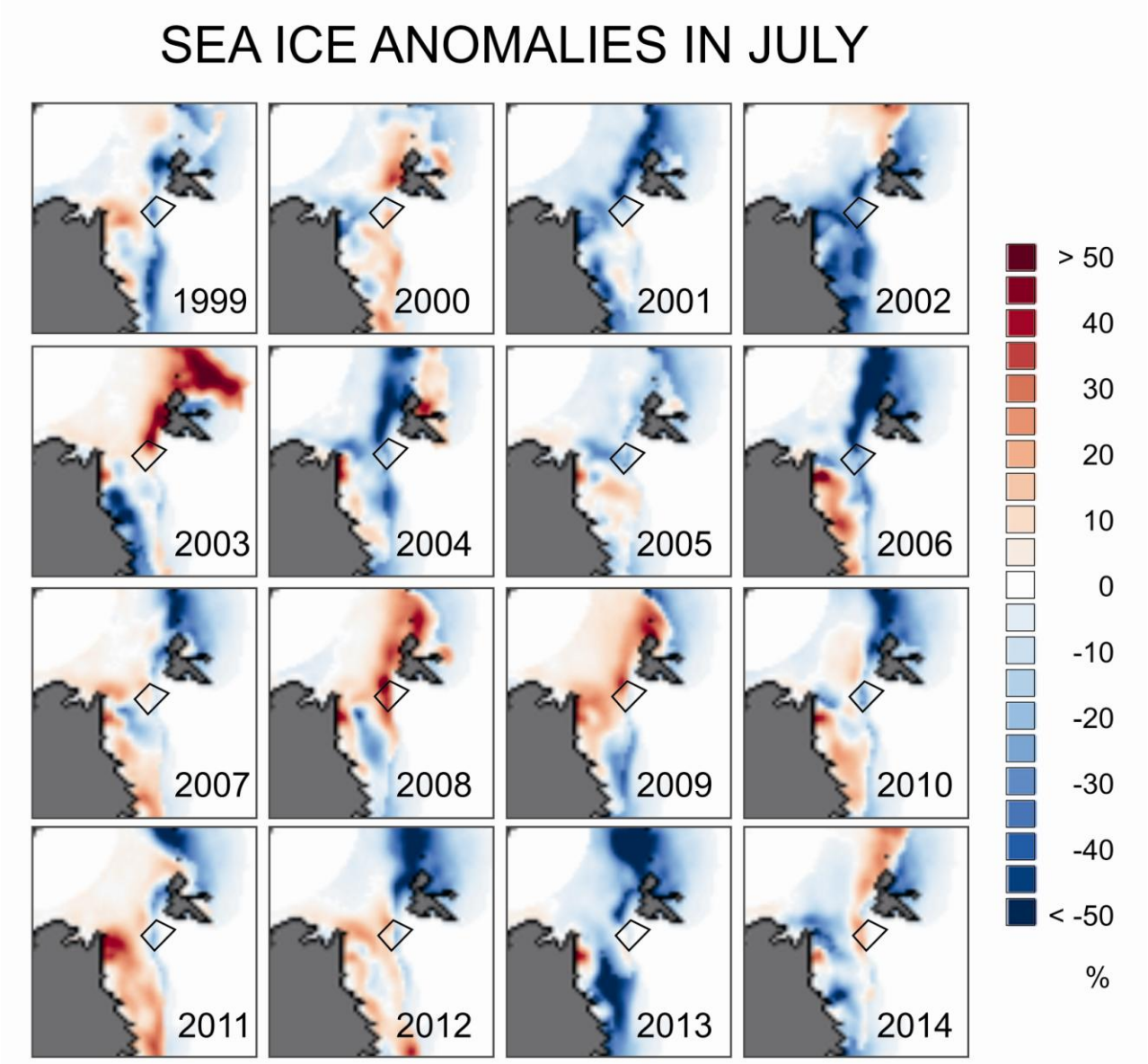

Fig. 2. Sea-ice anomalies from a 30-year reference period (1981-2000) in the greater Fram Strait for 1999 through 2014 (provided by the National Snow & Ice Data center, NSIDC); the trapezoid depicts the HAUSGARTEN area.

Based on measurements by an array of oceanographic moorings at 78°50′N in the Fram Strait, Beszczynska-Möller et al. (2012) studied the variability in Atlantic Water (AW) temperature and volume transport in the West Spitsbergen Current (WSC). For the time period 1997-2010, they calculated a positive linear trend in the AW mean temperature of 0.06°C per year, but no statistically significant trend was observed in the volume transport. Although comparing completely different water masses, annual mean temperatures at 250 m

and 2,500 m water depth showed constantly increasing values of about 1°C at shallow depths and approx. 0.1°C at the deep seafloor, respectively (Fig. 3).

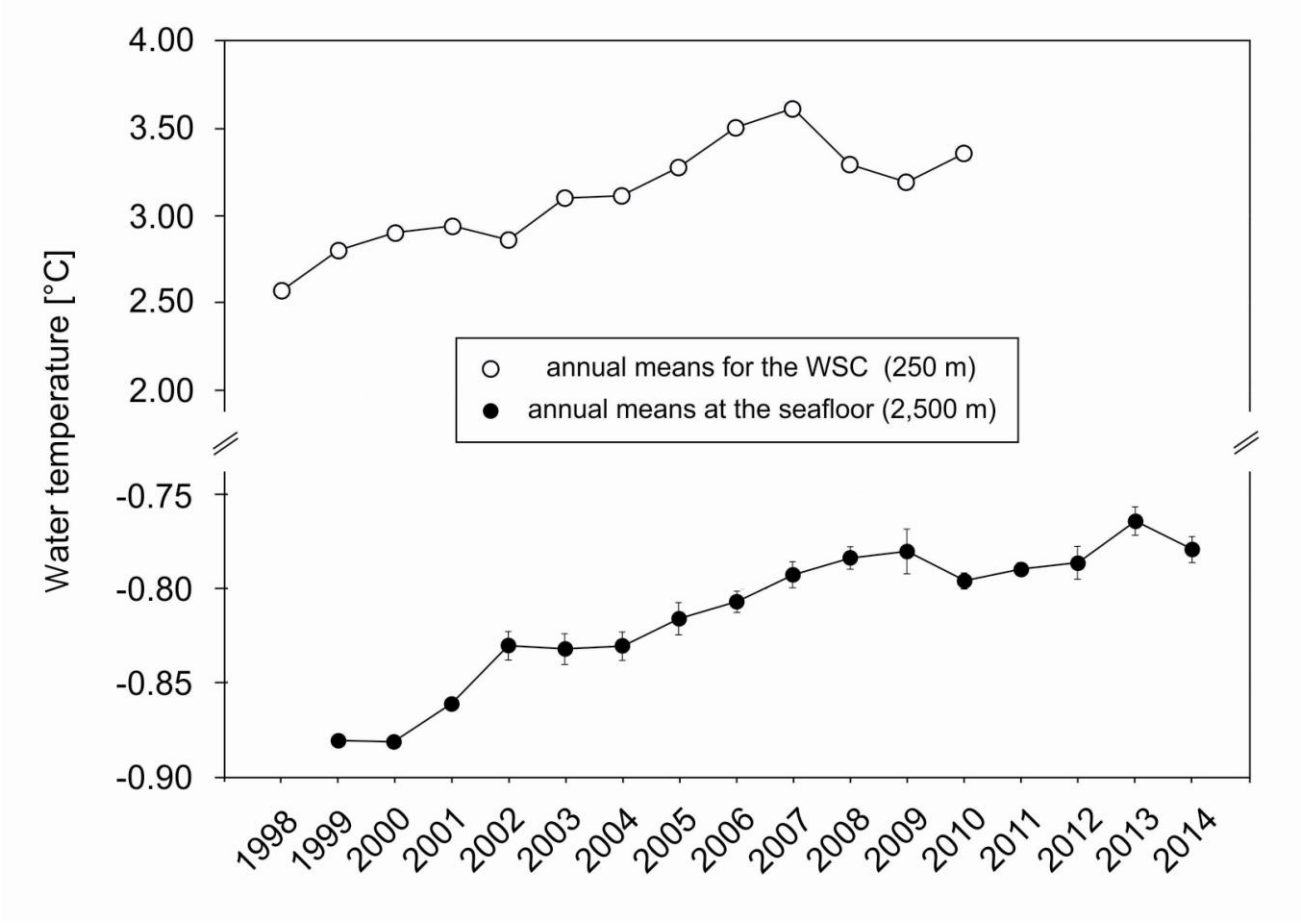

Fig. 3. Water temperatures in the eastern Fram Strait between 1998 and 2014; annual means in the WSC at 250 m (data from Beszczynska-Möller et al., 2012; top) and at 2,500 m water depth at the central HAUSGARTEN site off Svalbard (Glover et al., 2010 and Soltwedel, *unpubl. data*; bottom).

Besides the overall trend, two Warm-water Anomalies (WWA) were found in the AW passing through the Fram Strait between 1997 and 2010 (Beszczynska-Möller et al., 2012). The initial WWA occurred in 1999-2000, while the second, more pronounced one arose in late 2004 and continued until 2008. Whereas the first anomaly occurred in a confined area in the central Fram Strait, the latter one covered large areas in eastern parts of the strait, i.e., within the central HAUSGARTEN area. During the peak of the second warming (in

September 2006), the anomalously warm AW, with temperatures >3°C, even reached the East Greenland Current and the upper slope east of Greenland. On the eastern side of the WSC, the AW warmer than 3°C was present at a depth of 250 m throughout the year, in contrast to earlier years when its occurrence was limited to the summer months (Beszczynska-Möller et al., 2012).

3. Time-series work at HAUSGARTEN

Time-series work in the open ocean and in the deep sea is logistically challenging due to the difficult accessibility of the area of interest, especially in polar regions. Thus, sampling is usually restricted and limited to small time windows when cruises by research ships can be performed, finally resulting in snapshot-like datasets. Seasonally performed time-series from the open ocean and the deep sea are very rare. Such restriction can partly be overcome by using remote-sensing techniques, and by the installation of long-term (e.g., annually) moored systems carrying autonomous instruments allowing year-round measurements and sampling (see below). However, because of methodological restrains (e.g., restrictions to remote-sensing due to clouds, missing long-term stability for biochemical sensors, and preservation of samples in autonomous sampling devices) the application of these techniques still has its limitations.

One of the key characteristics of the scientific work at the LTER observatory HAUSGARTEN is the multidisciplinary approach, combining expertise from biologists, geochemists, sedimentologists, and physical oceanographers. International collaboration has been initiated in all fields where in-house experience was missing. An overview of key variables regularly assessed at HAUSGARTEN is presented in Table 1.

Table 1. Key variables regularly assessed at the LTER observatory HAUSGARTEN.

	Parameters	Pelagic Zone	Sediment-Water-Interface	Sediment
abiotic	temperature	X	X	
	oxygen	X	X	X
	currents (speed, direction)	X	X	
	sediment grain sizes, porosity			X
biotic	phyto-/zooplankton (abundance, diversity)	X		
	particle flux rate (mainly phytodetritial matter)	X		X
	biomarker in settling matter (marine, terrigenous)			X
	sediment-bound organic carbon (content, remineralization)		X	X
	bacteria (activity, abundance, biomass, diversity)	X		X
	meio-, macro-, megafauna (activity, abundance, biomass, diversity)			X
	demersal fish (activity, abundance, biomass, diversity)			X

Water column studies at HAUSGARTEN include the assessment of physico-chemical parameters, plankton communities as well as flux measurements of particulate matter to the deep seafloor. An Autonomous Underwater Vehicle (AUV) equipped with water samplers and various sensors (e.g., a CTD as well as sensors for oxygen, nitrate, chlorophyll *a*, pCO_2, CDOM, and PAR) is used for upper water column studies (Wulff et al., 2013). Phyto- and zooplankton are sampled with water collectors and different nets (e.g., Multi-net, Bongo-net); analyses focus on species composition, abundance and spatial distribution. The settling of particles to the seafloor is assessed with conical sediment traps with an opening of 0.5 m^2 and equipped with 20 sampling cups (see Kremling et al., 1996). Samples are poisoned *in situ* with mercuric chloride for the preservation of samples during and after deployment. Treatment of the samples in the laboratory follows the description in v. Bodungen et al.

(1991) and included the removal of so-called 'swimmers', i.e., zooplankton organisms that most probably enter the sediment traps actively (Harbison and Gilmer, 1986; Lee et al., 1989). Moorings and free-falling systems (bottom-lander), used as stationary platforms for observations and *in situ* experiments, are generally equipped with current meters and optodes to assess variations in hydrographic variables and oxygen concentrations, respectively.

Benthic communities are investigated over the entire size spectra from bacteria, meio- and macrofauna up to megafauna and demersal fish. Bacteria as well as meio- and macrobenthic organisms are sampled by multiple corer and box corer. Towed photo/video systems allow the non-invasive assessment of large-scale distribution patterns of epi/megabenthic organisms (for sampling procedures and sample processing, see Hoste et al. [2007], Budaeva et al. [2008], Bergmann et al. [2011], and Jacob et al. [2013]). Benthic studies at the HAUSGARTEN observatory also include biochemical analyses of sediment samples to estimate the input of phytodetritial matter to the seafloor as a food/energy source, as well as to assess activities and biomasses of the small sediment-inhabiting biota (for analytical methods see Hasemann et al., 2013). Microprofiler and benthic chambers attached to free-falling systems (bottom-lander) are used to study remineralization rates and exchange processes at the sediment-water interface. Remotely Operated Vehicles (ROV) are routinely used at two-year intervals to carry out observations and targeted sampling, to position and service autonomous instruments, and to conduct *in situ* experiments at the deep seafloor.

The data presented in the following sections reflects the current state of progress in the processing of samples from the various compartments of the marine ecosystem at the LTER observatory HAUSGARTEN. For example, while results from the very labor-intensive meiofauna studies are only available until 2009, data sets from faster, straight-forward analyses cover also the most recent years. In any case, results presented below cover at least a decade of multidisciplinary time-series work at HAUSGARTEN.

3.1 Pelagic studies

In the upper pelagic system, the development of phytoplankton biomass was investigated via chlorophyll *a* concentrations derived from satellite data (April through August between 1998 and 2012) and chlorophyll *a* concentrations sampled and processed from discrete water depths in the sunlit surface waters during summer expeditions to the HAUSGARTEN observatory. The chlorophyll *a* concentrations obtained with remote-sensing observations by the NASA sensors SeaWIFS and MODIS, and the ESA sensor MERIS, were merged to one CHL data product (GlobColour product, see http://hermes.acri.fr). Chlorophyll *a* in the West Spitsbergen Current (WSC) during the years 1998-2012 stayed relatively constant; however, a slight increase of the chlorophyll *a* biomass in the last years is visible in the satellite data (Fig. 4) as well as in the water column (data not shown), pointing to a phytoplankton biomass increase following the WWA in the Fram Strait between 2005 and 2008.

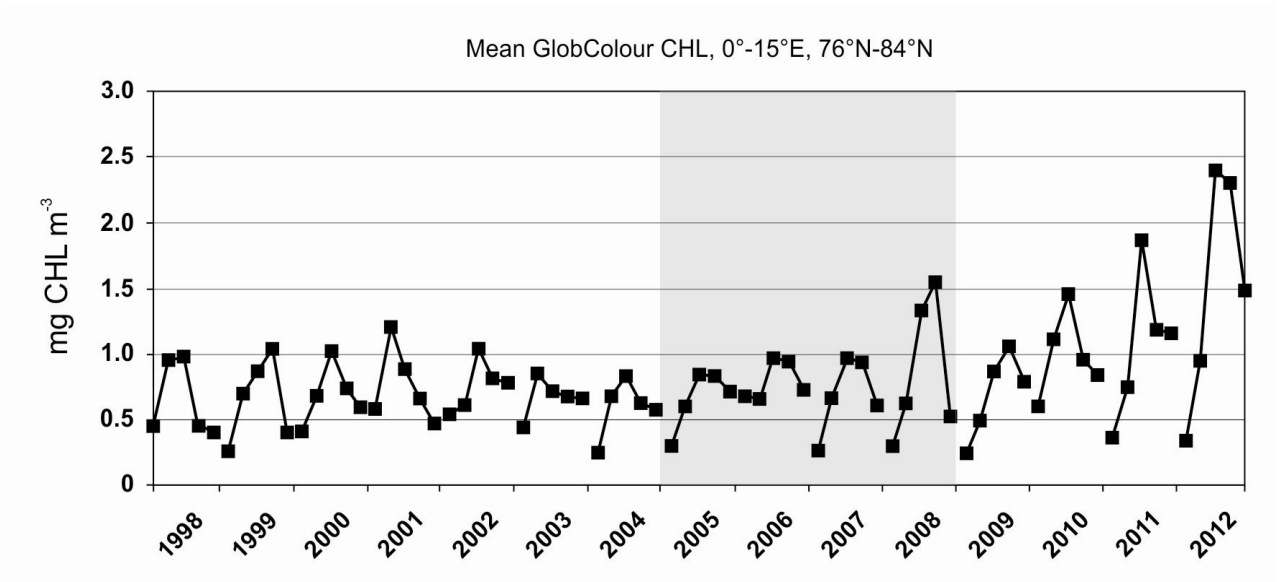

Fig. 4. Monthly means of satellite-retrieved chlorophyll *a* from the GlobColour product (CHL) averaged for an area in the West Spitsbergen Current (76°N - 84°N and 0° - 15°E) for growth periods covering the months April through August between 1998 and 2012. The gray-shaded area indicates the period of the Warm-Water-Anomaly (WWA).

Cherkasheva et al. (2014) found no direct link between sea-ice concentrations and chlorophyll *a* concentrations for the wider Fram Strait region. Therefore, the authors considered additional physical factors potentially affecting phytoplankton distribution, including sea-ice thickness, water temperatures, and salinity gradients from a validated sea-ice ocean circulation model (NAOSIM); the latter data were then used to calculate the time-series of stratification within this region. Results showed that the Marginal Ice Zone (MIZ) was promoting phytoplankton growth by stratifying the water column and potentially seeding phytoplankton communities. In this zone, the highest mean chlorophyll concentrations reached up to 0.8 mg CHL m^{-3} (average values for the productive season April-August). In the open ocean, the phytoplankton variability correlated best with stratification formed by solar heating of the upper ocean layers (Cherkasheva et al., 2014). The coastal zone around Svalbard showed processes associated with the presence of coastal ice that is suppressing rather than promoting the phytoplankton growth. During 12 years of observations, chlorophyll concentrations increased in the southern part of the Fram Strait, associated with an increase in sea-surface temperature and a decrease in Svalbard coastal ice (Cherkasheva et al., 2014).

The species composition of unicellular plankton organisms has been determined by collecting water samples from the chlorophyll *a* maximum layer at the HAUSGARTEN central station during summer months between 1998 and 2011 (Mebrahtom Kidane, 2011). In the years 1998 and 2003, diatoms of the genus *Thalassiosira*, *Chaetoceros*, and *Fragilariopsis* dominated the phytoplankton (Fig. 5).

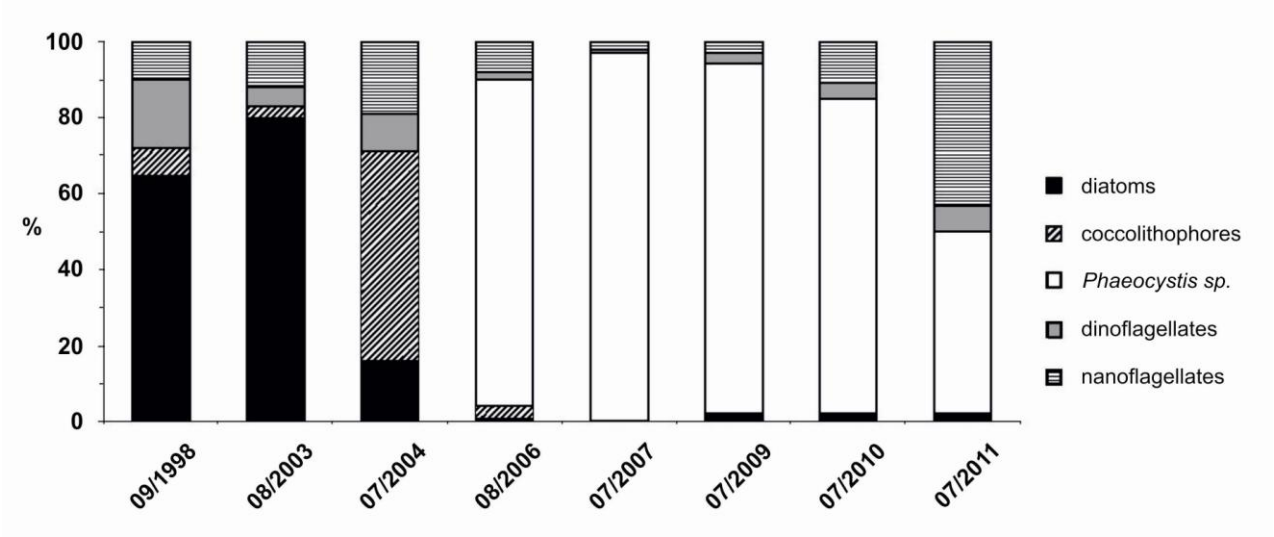

Fig. 5. Composition of unicellular planktonic protists (>3 µm) in the chlorophyll *a* maximum of the water column at the central HAUSGARTEN site for eight years from 1998 to 2011.

These years were characterized by longer periods of sea-ice coverage and comparably cold temperatures in surface waters. Coccolithophores, mainly composed of *Emiliania huxleyi*, prevailed in the samples from 2004. Throughout the following years, i.e., during and after the WWA, phytoplankton was dominated by the prymnesiophyte *Phaeocystis pouchetii*. Concomitant to the shift in phytoplankton composition, we noted an increase in protozooplankton abundance (e.g., ciliates and tintinnids) in the water samples. The observed changes in the species composition of unicellular planktonic protists is also partly reflected in the composition of the settling matter in sediment traps at the central HAUSGARTEN site, indicating modifications also in element cycling in the Arctic Ocean (see Section 3.2).

3.2 Flux studies

Results from sediment trap deployments indicate a co-variation of the total particulate matter flux and the share of biogenic matter within the overall flux with the prevailing ice conditions. Fluxes of total matter and components thereof (i.e., carbonate, particulate organic

carbon and nitrogen, biogenic particulate silica and biomarkers, e.g., brassicasterol, campesterol, β-sitosterol, long-chain alkenones, IP_{25}) revealed a bimodal seasonal pattern showing elevated sedimentation rates during May/June and at the end of the growth season in August/September (Bauerfeind et al., 2009; Lalande et al., 2013).

The total dry weight (DW) of settling matter over the years was rather constant, except for 2003 as well as 2008 and 2009, where DW values were slightly elevated (data not shown). The export flux of particulate organic carbon (POC) was rather low (2-3 g C m^{-2} a^{-1}) suggesting a large retention and recycling of the POC in the water above 200-300 m. Unexpectedly, fluxes of POC in the upper water column did not change significantly between 2000 and 2012, whereas the flux of biogenic particulate silica, a proxy for diatoms, decreased markedly from ~1.5 to <0.5 g m^{-2} a^{-1}, thereby indicating a shift in the dominant primary producers towards non-diatom organisms (Bauerfeind et al., 2009; Lalande et al., 2013). The annual flux of all biogenic components (i.e., opal + organic carbon + carbonate) between 2000 and 2012 varied between 8.6 and 15.7 g m^{-2} a^{-1}, and was almost constant before 2008/09, but increased following the WWA (Fig. 6, top).

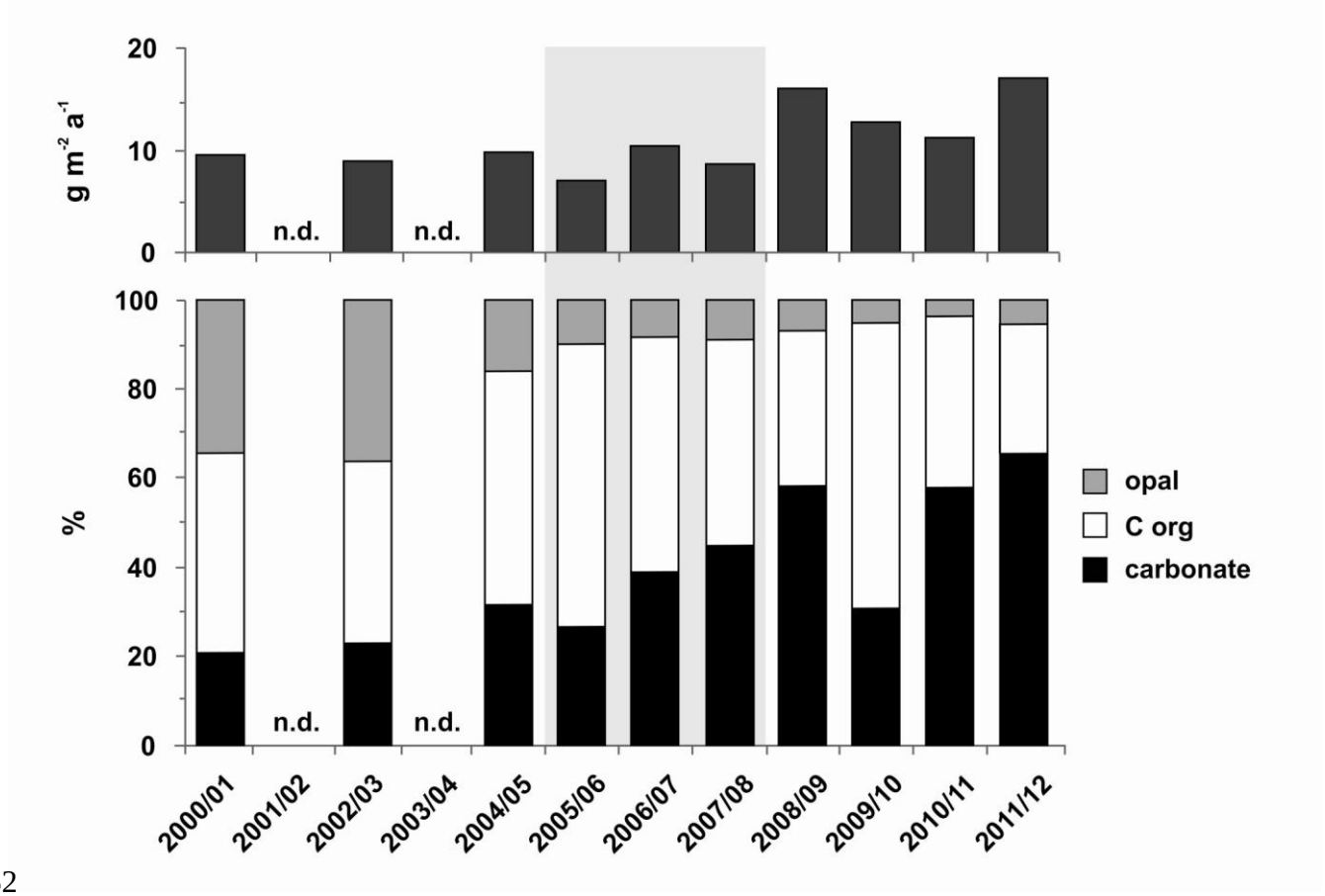

Fig. 6. Annual flux of biogenic matter (top) and percentage composition of its components (bottom) between 2000 and 2012 (n.d. = no data). The gray-shaded area indicates the period of the WWA.

The relative contribution of the biogenic components indicate that the proportion of opal decreased markedly to 10% or less, whereas the proportion of carbonate increased from 20-30% in the first years to >50% after the WWA (Fig. 6, bottom). The proportion of organic carbon varied from 30 to 60% and generally showed no clear trend between 2000 and 2012. An exception was the period 2009/2010 when carbonate and organic carbon contributed with ~30% and ~60%, respectively, to the flux of biogenic matter. However, this may be explained by the deviating depth of the sediment trap which, by accident, was installed ~120 m shallower compared to the other years.

The annual fluxes of brassicasterol, a biomarker for phytoplankton of marine and/or fluvial origin (Fahl and Nöthig, 2007; Fahl and Stein, 2012 and references therein), showed constant

values, except for 2006/2007, where brassicasterol concentrations in the settling matter were clearly higher (Fig. 7, top).

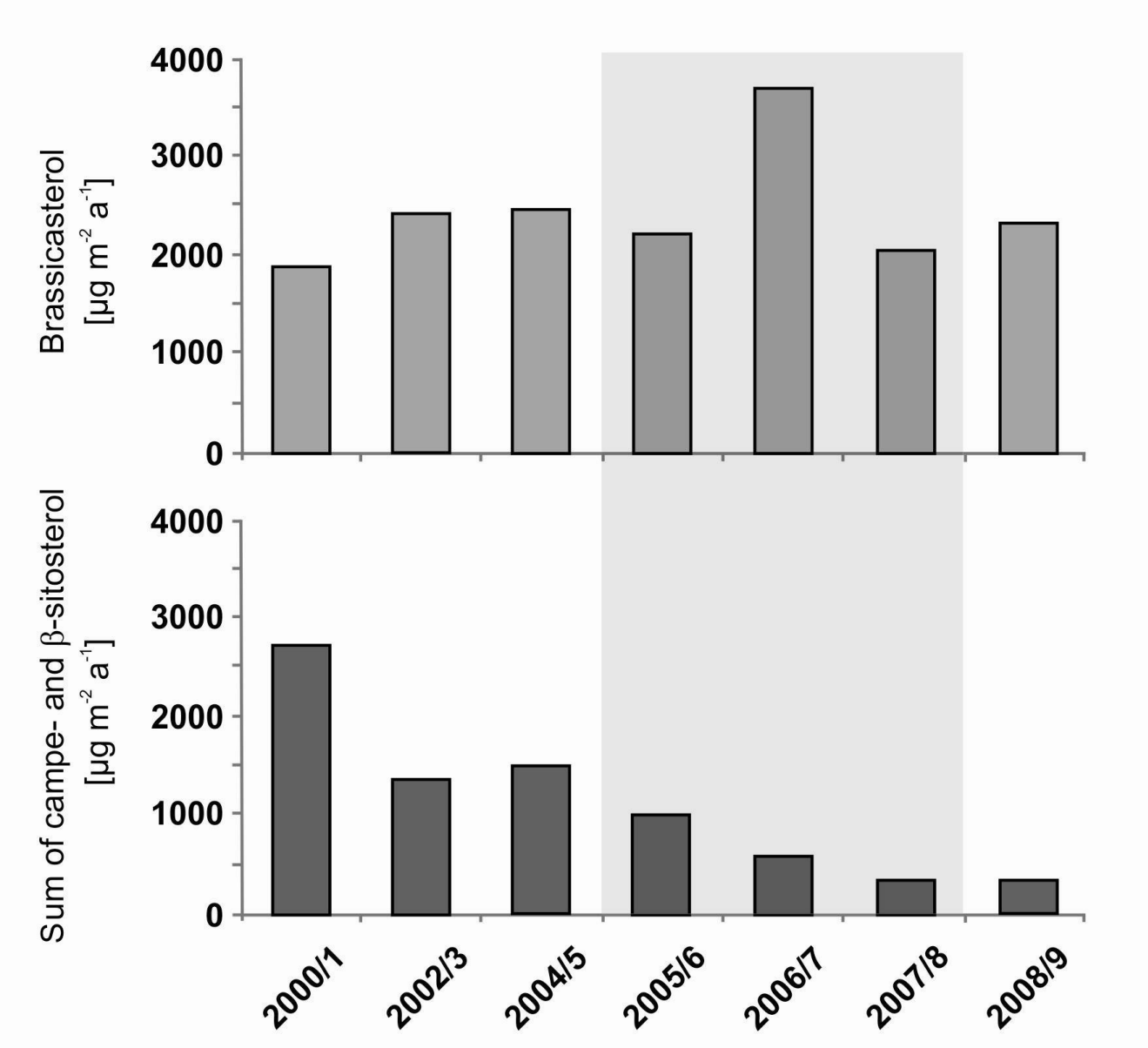

Fig. 7. Annual flux of the biomarker brassicasterol (top) and the sum of campesterol and β-sitosterol (bottom) for seven years between 2000 and 2009. The gray-shaded area indicates the period of the WWA.

The overall persistent flux over the last years may indicate a mixed signal related to phytoplankton input from the water column and ice-transported material via the Transpolar

Drift. In contrast, biomarkers for terrigenous origin (i.e., campesterol and β-sitosterol) decreased continuously between 2000 and 2009 (Fig. 7, bottom). A similar trend was found for the biomarker IP_{25} (data not shown), a highly branched isoprenoid with 25 carbons, which is biosynthesized exclusively by diatoms living in arctic sea-ice (Belt et al., 2007; Müller et al., 2009). Considering that the terrigenous organic matter in the HAUSGARTEN area is derived by ice transport from the arctic marginal seas (e.g., the Laptev Sea), the good correlation between the decreasing fluxes of IP_{25} (a sea-ice marker) and the terrigenous sterols campesterol and β-sitosterol is probably indicative of a generally decreasing sea-ice cover and thinner ice in the central Artic Ocean.

Differences in the export of protist assemblages during the period of highest flux in September were assessed by using the Terminal Restriction Fragment Length Polymorphism (T-RFLP) method (Marsh, 1999), which is based on sequence heterogeneity, e.g., within the 18S rDNA of different taxa. The composition of differently-sized restriction fragments in a sample acts as a characteristic fingerprint of a microbial community that allows qualitative comparisons of community compositions. A multidimensional scaling (metaMDS) plot based on T-RFLP differences in the exported protist assemblages at the central HAUSGARTEN site (79°N, 04°E) between 2000 and 2010 suggests that the community profiles segregate into four groups (Fig. 8). Group one is composed of samples collected in 2000 to 2002, group two in 2004 to 2005, group three in 2006 to 2007, and group four in 2008 to 2010. An ANOSIM analysis to test the significance of the *a priori* defined groups resulted in an R-value of 0.9256 and a *p*-value of 0.001, indicating highly significant differences between the defined groups. The metaMDS plot also implies that the protist communities in 2006-2010 were more similar to each other than to those of the years before the WWA (Fig. 8).

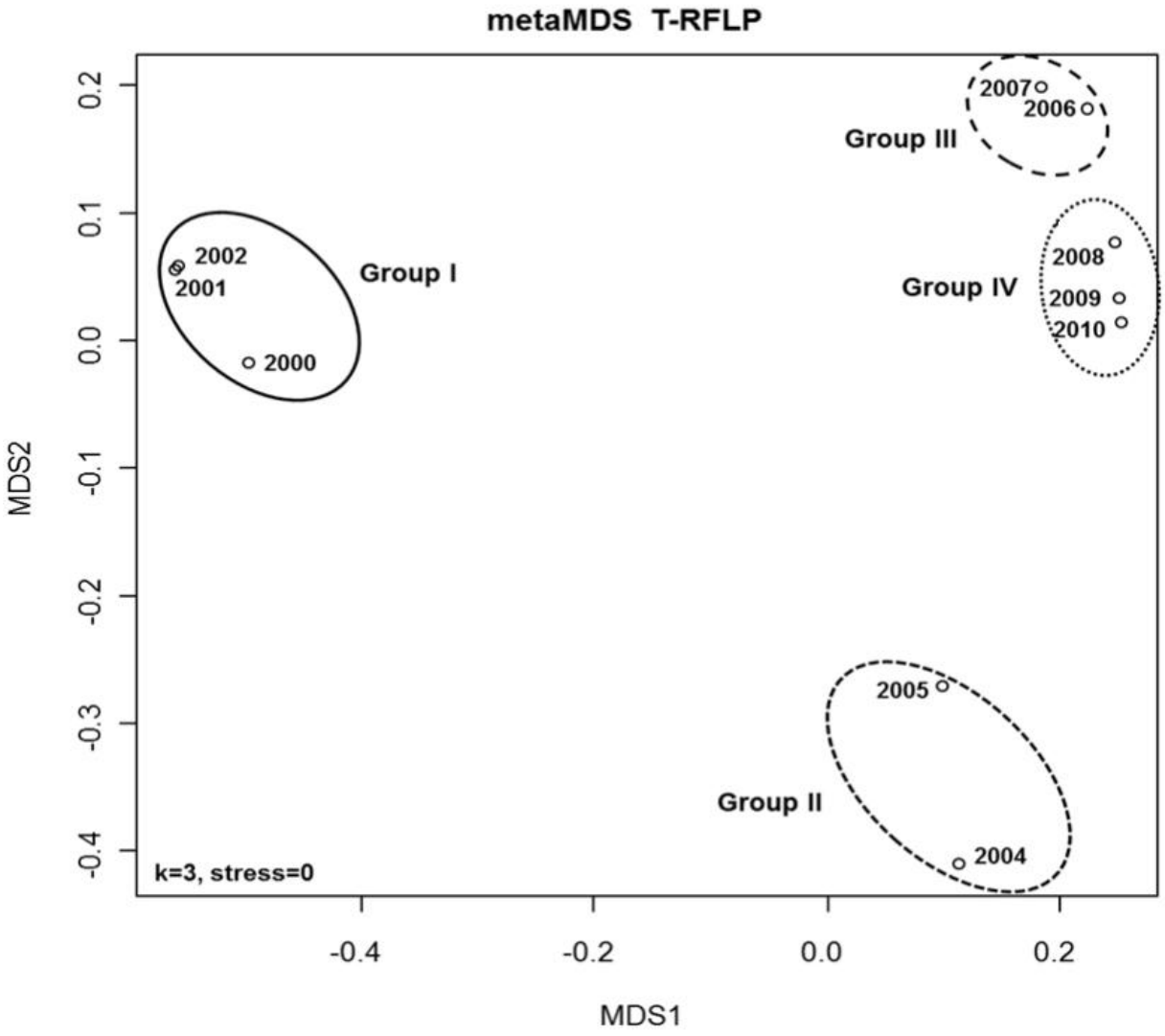

Fig. 8. Multidimensional scaling (metaMDS) plot to illustrate differences between the 18S T-RFLP patterns of the different protist communities in the sediment traps. The plot is based on the calculation of Jaccard indices for the data set derived from amplification of an 18S rDNA fragment and subsequent digestion with the restriction enzyme HaeIII.

Valuable information about the composition of the zooplankton community in the HAUSGARTEN area can be achieved by analyzing the composition of swimmers that are caught as a bycatch in the sediment traps (e.g., Seiler and Brand, 1997; Willis et al., 2008; Kraft et al., 2011; Bauerfeind et al., 2014). At the HAUSGARTEN, we analyzed changes in the abundance of two major groups, i.e. pelagic amphipods (species of the genus *Themisto*) and gastropods (thecosome pteropods of the genus *Limacina).*

Within the amphipods, three *Themisto* species were observed regularly and in great abundance, i.e., the arctic species *Themisto libellula*, the sub-arctic *T. abyssorum*, and the North Atlantic species *T. compressa* (Kraft et al., 2012). The pteropod species consisted of the polar species *Limacina helicina* and the transitional, boreal warm water-adapted *L. retroversa* (Bauerfeind et al., 2014). The occurrence and composition of these organisms in the samples underwent substantial changes during the period 2000-2012 (Fig. 9). Pteropod numbers increased significantly during the WWA, showed comparably low values in 2009/2010, but steeply increased again until the end of the time-series (Bauerfeind et al., 2014; Busch et al., 2015). The overall rise in pteropods numbers was accompanied by a switch in dominance of species from the cold-adapted *L. helicina* that dominated in the first years until 2004/2005 towards the warm water-species *L. retroversa* in the subsequent years (Fig. 9, top).

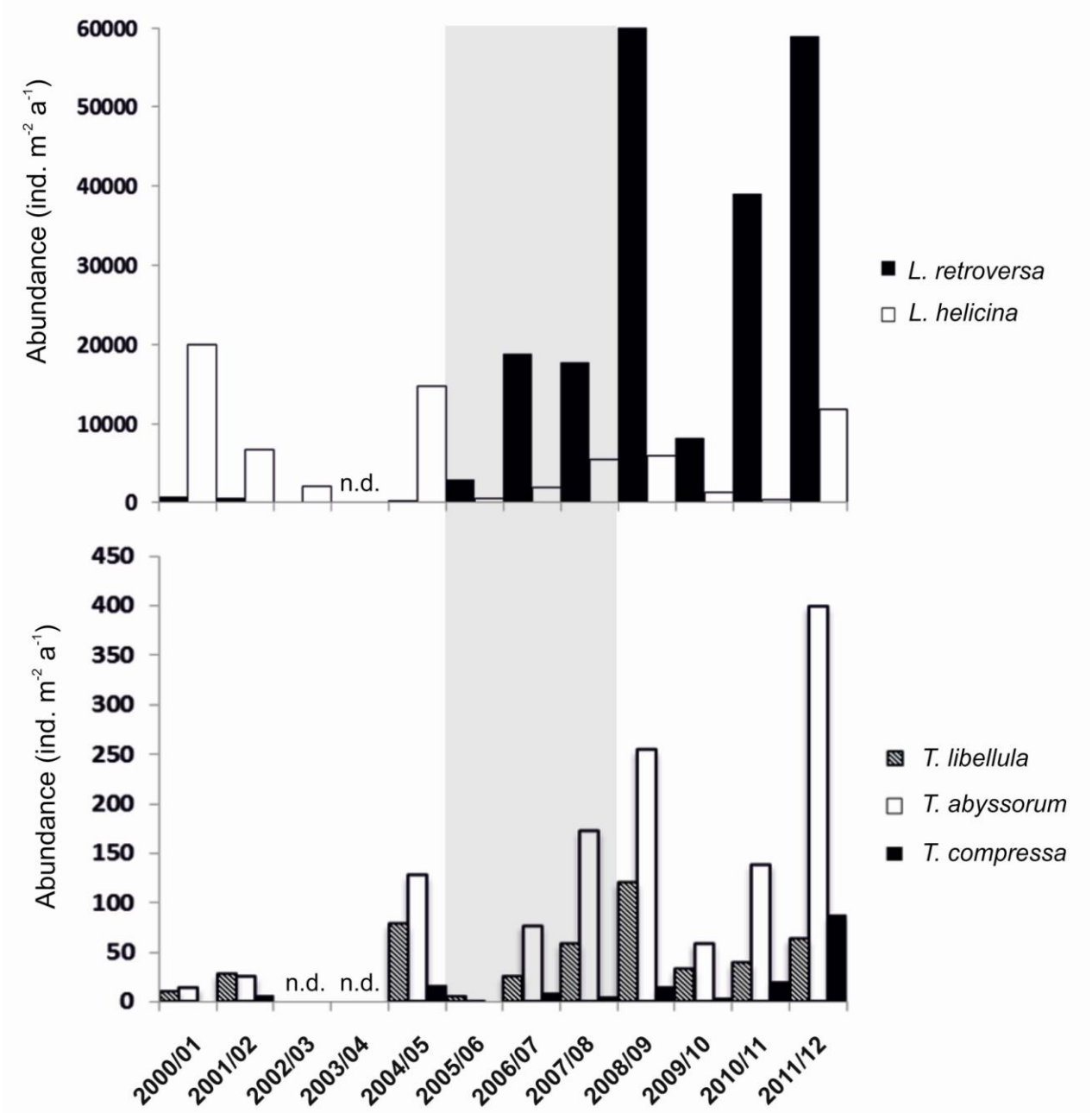

Fig. 9. Abundance of *Limacina* pteropods (top) and *Themisto* amphipods (bottom) in the sediment traps at the central HAUSGARTEN site (n.d. = no data). The gray-shaded area indicates the period of the WWA.

The number of amphipods also increased steadily (Fig. 9, bottom), mainly due to increased numbers of the sub-arctic species *T. abyssorum*. The arctic species *T. libellula*, on the other hand, did not follow the general trend after the WWA, but was present in varying abundances during all the years since 2000. Most remarkably, we also noted the occurrence of *T.*

compressa, an amphipod species, which has not been recorded in the Fram Strait before. This species was first observed sporadically during 2001-2005, and was present continuously in the subsequent years with largest numbers in 2011, when also juveniles of the species were recorded for the first time (Kraft et al., 2013).

3.3 Benthic studies

3.3.1 Biogenic sediment compounds

Benthic long-term studies at HAUSGARTEN include the analyses of biogenic sediment compounds to estimate food availability at the deep seafloor and the biomass of the small benthic biota. The input of phytodetritus, representing the main food source for benthic organisms, is estimated by analyzing concentrations of sediment-bound chloroplastic pigments (Yentsch and Menzel, 1963; Holm-Hansen et al., 1965). As the fluorometric method used in our studies does not discriminate between individual breakdown products, we prefer the term chloroplastic pigment equivalents (CPE) for the bulk pigments analyzed (Thiel, 1978). Benthic biomass within the sediments was determined by different biochemical assays. Particulate proteins, indicating the bulk of "living" and "dead biomass", i.e. small organisms and detrital matter, respectively, were analyzed photometrically (Greiser and Faubel, 1988). The analysis of sediment-bound phospholipids (indicative of cellular membranes) provides biomass estimates for benthic micro-organisms (Findlay et al., 1989). According to the sample sizes used for these studies, biomass estimations cover the entire small-sized benthic biota, including bacteria, fungi, protozoans, and the metazoan meiofauna.

Spatial and temporal assessments of biogenic sediment compounds along the bathymetric HAUSGARTEN transect off Svalbard showed generally decreasing values with increasing water depth, but also distinct interannual variations between 2000 and 2010. Hovmöller

diagrams displaying anomalies from ten year means reveal a sharp increase in sediment-bound pigment concentration, i.e., phytodetritial matter between 2006 and 2007 (Fig. 10, left).

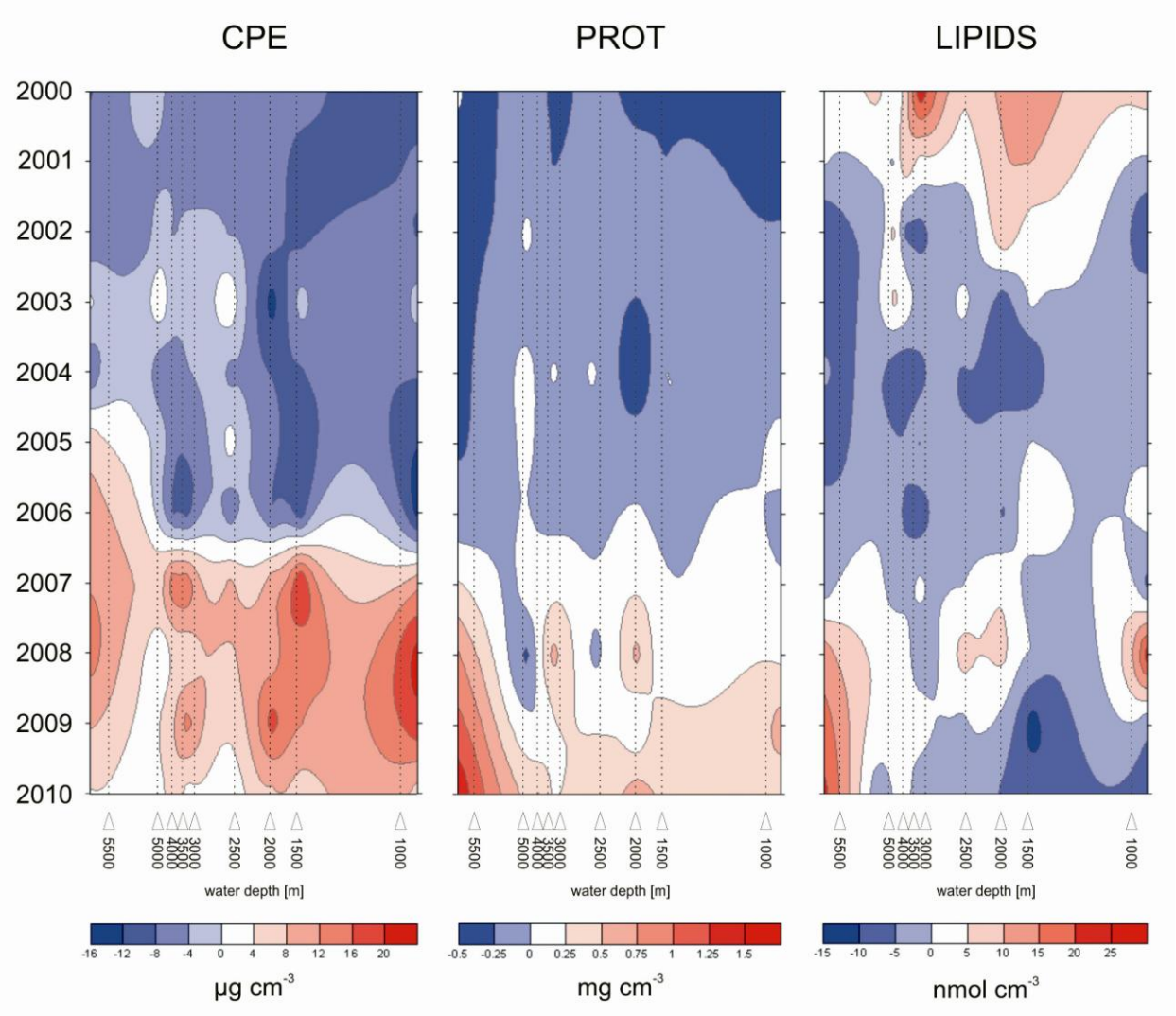

Fig. 10. Spatio-temporal diagrams of interannual variability in different biogenic sediment compounds along the bathymetric transect off Svalbard between 2000 and 2010: anomalies from the long-term mean in sediment-bound chloroplastic pigments (CPE), particulate proteins (PROT), and phospholipids (LIPIDS); blue colors = lower values, white and red colors = values exceeding the long-term mean.

At the same time, during the peak of the WWA, a similar but less pronounced shift to positive values was found for particulate proteins (total biomass), whereas phospholipid concentrations (microbial biomass) followed the trend only vaguely. While strong positive

values were found at the onset of the time-series study (where pigment and protein concentrations were already low), enhanced microbial biomass values since 2007 were only found for certain water depths (Fig. 10, right). Differences in food quality at the beginning of the time-series and after the increased phytodetritial matter availability at the deep seafloor following the WWA might obscure a clear relationship.

3.3.2 Life at the deep seafloor

Benthic bacteria at HAUSGARTEN were assessed using a LIVE/DEAD® *Bac*Light™ Bacterial Viability Kit protocol adapted to marine sediments (Quéric et al., 2004). Along the bathymetric transect off Svalbard, the analyses revealed a decrease of both bacterial viability and abundance with increasing water depth. Maximum bacterial abundance (4.9-5.4 x 10^8 cells cm^{-3}) was found in the uppermost sediment layer at ~1,250 m water depth; lowest bacterial cell numbers (0.8-1.2 x 10^8 cells cm^{-3}) were observed at the deepest stations (~5,600 m water depth). The percentage of viable (and thus potentially active) cells ranged between 20-60% within the first, and 10-40% within the fifth centimeter of sediment throughout the transect (Quéric et al., 2004).

Regional distribution patterns of the benthic bacterial community at HAUSGARTEN were examined by Jacob et al. (2013). Samples from 13 stations were retrieved from the bathymetric (1,284-3,535 m water depth, 54 km in length) and the latitudinal transect (~2,500 m water depth; ~120 km in length) (see Fig. 1). Applying the 454 Massively Parallel Tag Sequencing (MPTS) method, Jacob et al. (2013) found a spatially highly diverse bacterial community, with strong water depth-related patterns in community structure along the bathymetric transect, whereas no significant changes in community structure were observed with increasing spatial distance along the latitudinal transect. MPTS identified a total of 41 phyla, 78 classes, 136 orders, 215 families, and 410 genera. Most of the bacteria belonged to

the phylum Proteobacteria (47%), with the most abundant classes being Gammaproteobacteria (23%), Deltaproteobacteria (15%), and Alphaproteobacteria (7%). The second most abundant phylum was Bacteroidetes (9%), including the classes Flavobacteria (3%) and Sphingobacteria (5%). Other abundant phyla were Actinobacteria (3%), Acidobacteria (5%), and Verrucomicrobia (4%). The richness of operational taxonomic units decreased substantially during the WWA in 2005-2007, and again increased in 2008 to a similar level as in 2003 (Jacob, 2014). Changes in the bacterial community were attributed to changes in food availability along the bathymetric transect as well as during the WWA (see Section 3.3).

Meiobenthic studies at HAUSGARTEN between 2000 and 2009 focused on the metazoan community and revealed densities ranging from 269 ± 119 to 3,248 ± 22 ind. 10 cm^{-2} (Hoste et al., 2007; Grzelak, 2015). Nematodes dominated the metazoan meiofauna at every depth and sampling year (85-99%), followed by harpacticoid copepods (up to 4.6%). The expected pattern of gradually decreasing meiobenthic densities with increasing water depth was not documented. Instead, the bathymetric transect at HAUSGARTEN could be roughly subdivided into a shallow part with both high nematode and copepod densities ranging between approximately 1,000 and 2,000 m water depth (means ± SD: 2,259 ± 157 nematodes 10 cm^{-2}, and 50 ± 4 copepods 10 cm^{-2}), and a deeper part between approximately 3,000 and 5,500 m water depth with clearly lower nematode and copepod densities (means ± SD: 595 ± 52 nematodes 10 cm^{-2}, and 11 ± 2 copepods 10 cm^{-2}). Compared to deep-sea studies from the North Atlantic, the nematode community at HAUSGARTEN is characterized by very high species numbers, even though the number of genera was in the same order of magnitude (Hoste, 2007). Rare genera and species were diverse, but represented <1% of the total nematode abundance. The overall nematode community structure at HAUSGARTEN was similar to other typical deep-sea communities, with dominant genera such as *Tricoma*, *Desmoscolex*, *Acantholaimus*, *Halalaimus* and members of the Monhysteridae. Except for the deepest stations, deposit feeders were dominant at each water depth followed by epistrate

feeders. The nematode community composition changed gradually with water depth. Differences were mainly due to variations in the relative abundance of genera rather than the presence/absence of genera. At the species level, some indicative species could be found at most water depths, especially within the Monhysteridae, Xyalidae, and Desmoscolecidae. Aside from water depth as the main factor accounting for differences in nematode communities, interannual variability in nematode community structure was apparent with high relative abundances of *Dichromadora*, *Microlaimus*, *Acantholaimus*, *Halalaimus*, *Daptonema*, and *Tricoma* related to enhanced food availability (Hoste, 2007). Since 2005, *Sabatieria* and *Sphaerolaimus* replaced *Microlaimus* and *Daptonema* in the list of the most abundant genera (Grzelak, 2015).

Combined data from Hoste et al. (2007) and Grzelak (2015) for the central HAUSGARTEN site between 2000 and 2009 showed an overall decrease in nematode densities from 2002 to 2005 and generally increased values in the subsequent years, with highest values in 2006 (Fig. 11). Moreover, based on the classification of the nematode communities into feeding types, we observed overall increasing trophic diversities (indicated by the Index of Trophic Diversity, ITD) at the central HAUSGARTEN station between 2000 and 2006, with highest diversity in 2006. Most probably affected by changes in food availability during the WWA (see Section 3.3), trophic diversity of the nematode communities clearly decreased in 2007, with an increasing trend in the following two years. The comparably high trophic diversity of the nematode communities in 2006 can be traced back to almost similar proportions of particle and epigrowth feeders together with a comparatively high proportion of predators/scavengers and omnivore feeding nematodes. The low trophic diversity in 2007 is mainly caused by the high dominance of non-selective particle feeders (up to 48%), whereas similar proportions of selective and non-selective particle feeders (between 31% and 37%) as well as comparatively high proportions of

predators/scavengers and omnivore feeding nematodes (between 8% and 11%) lead to the increasing trophic diversity in the years 2008 and 2009.

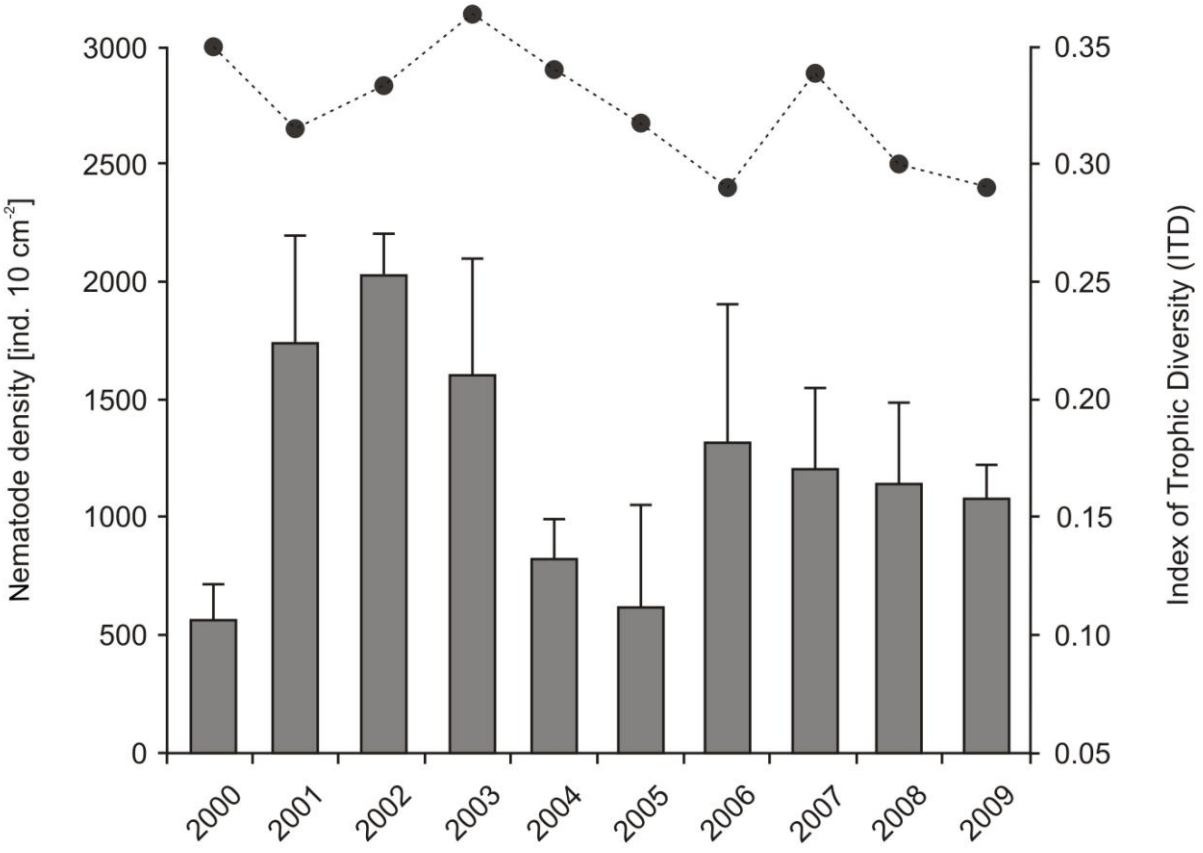

Fig. 11. Mean nematode densities and standard deviations from three replicates (bars), and trophic diversity (bullets) of the nematode community inhabiting sediments from the central HAUSGARTEN site (~2,500 m water depth) off Svalbard from 2000 to 2009.

Macrofauna were only irregularly sampled at HAUSGARTEN, so far not allowing the study of temporal variations in the area. However, spatial studies revealed distinct depth-related, but also horizontal differences in macrofaunal community structure.

Along a transect towards the Kongsfjorden (Svalbard), Włodarska-Kowalczuk et al. (2004) found a community replacement along the depth gradient with four different types of assemblages categorized as SHELF (<370 m), SHALLOW SLOPE (~500 m), DEEP SLOPE

(~1,500 m), and RISE (>2,000 m). The dominant macrofauna taxa in different depth zones along the bathymetric transect are summarized in Table 2.

Table 2. Dominant macrofauna taxa at different depth zones along the bathymetric transect in the eastern Fram Strait (in brackets: relative proportion from the entire macrofauna community; P = Polychaeta, C = Crustacea, B = Bivalvia, E = Echinodermata, S = Sipunculida).

SHELF (<370 m)	**SHALLOW SLOPE** (~500 m)	**DEEP SLOPE** (~1500 m)	**RISE** (>2000 m)
Prionospio cirrifera (23.5%), **P**	*Yoldiella lucida* (8.9%), **B**	*Thyasira dunbari* (22.5%), **B**	*Myriochele heeri* (25.8%), **P**
Cossura longocirrata (17.7%), **P**	*Exogone* cf. *verugera* (8.5%), **P**	*Aricidea* ssp. (16.8%), **P**	*Myriochele fragilis* (16.3%), **P**
Lumbrineris sp. (12.5%), **P**	*Leucon nathorsti* (5.1%), **C**	*Paraonis* sp. / *Paradoneis* sp. (5.6%), **P**	*Paraonis* sp. / *Paradoneis* sp. (9.5%), **P**
Leitoscoloplos sp. (10.2%), **P**	*Chone paucibranchiata* (4.7%), **P**	*Ophiura* juv. (4.6%), **E**	*Notomastus* sp. (7.1%), **P**
Chaetozone group (7.7%), **P**	*Tanaidacea* sp. A (4.3%), **C**	*Myriochele fragilis* (3.5%), **P**	*Sipunculida* nd (5.0%), **S**
Levinsenia gracialis (3.5%), **P**	*Nicomache* sp. (4.1%), **P**	*Ilyarachnidae* nd (3.2%), **C**	*Tanaidacea* sp. A (4.0%), **C**
Ophiura robusta (3.0%), **E**	*Tanaidacea* sp. B (3.9%), **C**	*Sipunculida* nd (3.2%), **S**	*Haustoriidae* nd (3.2%), **C**
Heteromastus filiformis (2.9%) **P**	*Nothria conchylega* (3.7%), **P**	*Capitellidae* nd (2.8%), **P**	*Yoldiella* sp. (3.0%), **B**
Myriochele oculata (1.5%), **P**	*Heteromastus filiformis* (3.0%), **P**	*Oedicerotidae* nd (2.5%), **C**	*Aricidea* ssp. (0.4%), **P**
Maldane sarsi (1.0%), **P**	*Ophiura* juv. (3.0%), **E**	*Tanaidacea* sp. A (1.8%), **C**	*Ilyarachnidae* nd (0.3%), **C**

Macrofaunal species richness (expressed by the number of species per sample) decreased with water depth. There was, however, no clear bathymetric pattern in diversity measures; the classic increase of species richness and diversity at mid-slope depths was not observed. According to Włodarska-Kowalczuk et al. (2004), Shannon-Wiener diversity was the highest at 525 m water depth ($H'_{(\log e)}$ = 3.54) and lowest at 2,025 m depth ($H'_{(\log e)}$ = 1.46). Species richness and diversity at the deep stations were much lower than in comparable studies from the temperate North Atlantic. Włodarska-Kowalczuk et al. (2004) related this finding to the geographic isolation of Greenland–Icelandic–Norwegian Seas from the Atlantic pool of species. Macrofaunal biomass was negatively correlated with depth (R = -0.86), and ranged from 61 g ww m^{-2} at the shallowest station sampled (212 m) to 1 g ww m^{-2} at 2,025 m water depth. Biomasses were much higher than at similar depths in the multi-year ice-covered High

Arctic (Kröncke, 1994; 1998), while resembling those from temperate and tropical localities (Flach et al., 1999; Galeron et al., 2000).

In their study on horizontal community patterns, Budaeva et al. (2008) used the nested sampling to study different scales of macrofauna distribution at three sampling sites along a 26-km long transect at 2,500 m close to the central HAUSGARTEN site. Two separate macrofaunal assemblages were identified. The first assemblage comprised individuals found in three box core samples taken at one of the three sites. The second assemblage contained all individuals collected with the other six box corers taken at the remaining two sites located about 2 km away from each other and 23 km away from the third site. Budaeva et al. (2008) compared their findings with the results published by Włodarska-Kowalczuk et al. (2004) and concluded that the macrobenthos in the HAUSGARTEN region appears to be organized at three spatial scales: communities that replace each other along the depth gradients, species assemblages that contribute to the heterogeneity within each vertical zone, and single-species patches that create variability at the local scale (Budaeva et al., 2008).

Large-scale distribution patterns of epi/megafauna organisms are regularly assessed by a towed photo/video system (Ocean Floor Observation System, OFOS). Investigations along the depth transect off Svalbard revealed a clear bathymetric zonation of megafaunal assemblages (Soltwedel et al., 2009). Megafaunal densities ranged between 11 and 38 ind. m^{-2} with highest densities at 1,650 m and lowest densities at 3,000 m depth. The number of taxa ranged between 4 at 5,500 m, and 27 at 1,650 m water depth. Deposit-feeding brittle stars (*Ophiocten* cf. *hastatum*) dominated the continental margins up to depths of ~1,300 m with mean densities of 17 ind. m^{-2}. At a station only 300 m deeper, small yet unidentified amphipods dominated the fauna (37 ind. m^{-2}). At ~2,500 m water depth, deposit-feeding sea cucumbers (*Kolga hyalina*) and suspension-feeding sea anemones accounted for the majority of megafauna (4 and 3 ind. m^{-2}, respectively). Suspension-feeding crinoids (*Bathycrinus carpenterii*, 5 ind. m^{-2}) and sea anemones (2 ind. m^{-2}) were the most abundant groups seen at

~3,000 m water depth. Small arctic sea cucumbers (*Elpidia heckeri*, 30 ind. m^{-2}) dominated the Molloy Hole. The zonation patterns appear to be controlled primarily by food availability (Soltwedel et al., 2009). Log_2-based Shannon-Wiener diversity ranged between 0.34 and 2.58 with highest densities at about 2,620 m ($H'_{(log\ 2)}$ = 2.58) and between 2,965 and 3,043 m ($H'_{(log\ 2)}$ = 2.50) water depths. Diversity was lowest at 1,642 to 1,688 m ($H'_{(log\ 2)}$ = 0.34) and between 5,333 and 5,404 m ($H'_{(log\ 2)}$ = 0.51).

Analysis of seafloor photographs taken at ~1,250 m and ~2,500 m water depth off Svalbard in the years 2002, 2004, 2007, and 2011/2012 revealed significant temporal variation in megafaunal densities and community composition (Fig. 12).

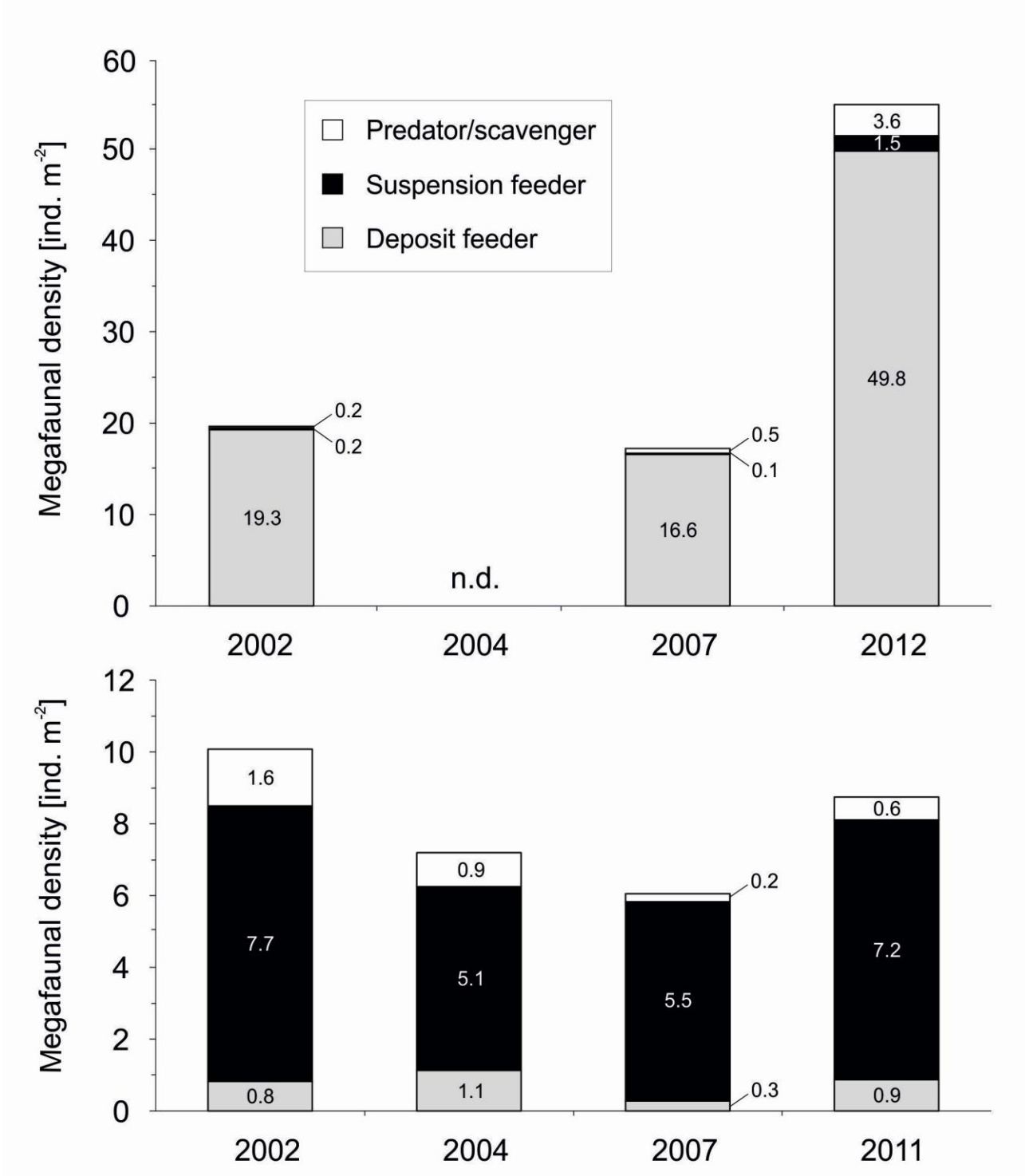

Fig. 12. Mean megafaunal densities in different feeding groups at ~1,250 m (top) and ~2,500 m water depth (bottom) between 2002 and 2012, and 2011, respectively. (n.d. = no data)

At the shallower site, megafaunal density was similar in 2002 and 2007, but significantly higher in 2012 (Kruskall-Wallis test, pairwise Mann-Whitney tests applying a Bonferroni

correction of $p = 0.017$; Fig. 12, top) (Meyer et al., 2013). OFOS footage taken at 2,500 m water depth indicated a significant gradual decrease in total megafaunal densities between 2002 and 2007 (Bergmann et al., 2011). While suspension-feeder densities also declined, predator/scavenger and deposit-feeder densities decreased to such a degree that suspension feeders made up >90% of the megafauna in 2007. After 2007, however, total megafaunal densities grew again verging on initial levels in 2011 (Fig. 12, bottom) (see also Müller et al., *this issue*). Overall, megafaunal densities from 2002 and 2011 were significantly higher than those recorded in 2004 and 2007 (Kruskall-Wallis test, pairwise Mann-Whitney tests with a Bonferroni correction $p < 0.001$).

4. Insights from 15 years of observations at HAUSGARTEN

HAUSGARTEN is synonymous with the longest multidisciplinary time-series study at a polar open-ocean site. Multidisciplinary studies at the LTER observatory covered almost all parts of the marine ecosystem and already exhibited a number of interesting temporal trends.

A warming event in the Atlantic Water layer in the eastern Fram Strait between 2005 and 2008 left a strong "footprint" in the arctic marine ecosystem in the HAUSGARTEN area. Impacts of the Warm-Water Anomaly (WWA) encompassed the increased growth of sub-arctic primary producers as well as a northward displacement, increased abundance and reproductive output of sub-arctic species, leading finally to changes in community structure due to range shifts. Cascading effects propagating through the entire food web led to an astoundingly rapid and far-reaching reaction of the entire open-ocean ecosystem from the pelagic to the deep seafloor. A number of variables monitored at the HAUSGARTEN observatory seem to fall back to their previous state subsequent to the WWA (e.g., decreasing proportions of *Phaeocystis pouchetii* between 2009 and 2011), while others seem to remain at a different level (e.g., constantly low amounts of diatoms and high densities of the sub-polar

pteropod species *Limacina retroversa* as well as the enduring occurrence of the North Atlantic amphipod species *T. compressa*). At least certain components of the marine ecosystem in the Fram Strait might have reached a "tipping point", i.e., a threshold in environmental forcing at which the future state of the system is qualitatively altered (Lenton et al., 2008).

It is a common knowledge that the Marginal Ice Zones (MIZ) are biologically very important (Sakshaug and Skjoldal, 1989), because stratification due to ice melting combined with a generally ample supply of nutrients sets the stage for vigorous phytoplankton production in the upper water layers. Zooplankton, pelagic fish, marine mammals and seabirds aggregate at the ice edge and exploit phytoplankton production in the MIZ. Large parts of the biological production in the MIZ sinks through the water column and forms a basis for rich communities of benthic organisms. Data collected at HAUSGARTEN showed that the proximity of the sea ice instantaneously positively affects the flux of particulate matter to the seafloor. In 2003 as well as in 2008 and 2009, when ice anomalies showed strong positive values, material collected in sediment traps at the central HAUSGARTEN site showed increased total dry weights, which could be attributed to increased amounts of lithogenic matter settling out during ice melt (Bauerfeind et al., 2009). Overall increased flux rates in biogenic particulate silica (a proxy for diatoms) and zooplankton fecal pellets in the presence of the ice cover at HAUSGARTEN were detected by Lalande et al. (2013). A close correlation between maximum sedimentation rates and the position of the ice edge was also shown by Ramseier et al. (1999) for mooring sites in the north-eastern Greenland Sea.

Although sea ice has the inherent potential to influence physico-chemical and biological processes in the water column (see above), most pronounced variations in the marine ecosystem at HAUSGARTEN appeared to be related to large-scale temporal variations in surface water temperature. A warm water anomaly (WWA) detected between 2005 and 2008 (Beszczynska-Möller et al., 2012) led to significant changes in planktonic protist assemblages and in unicellular phytoplankton communities (Mebrahtom Kidane, 2011). While

macroscopic and biochemical analyses on sediment trap material revealed an overall decrease in diatoms since the beginning of the time-series studies at HAUSGARTEN, the WWA induced an abrupt shift in phytoplankton to a community dominated by micro- and nanoflagellates. A general shift from a dominance of diatoms to a dominance of picoplankton in a warmer Arctic Ocean is commonly predicted (Morán et al., 2009) and already supported by observations in the central Arctic Ocean (Li et al., 2009; Zhang et al., 2015).

Increasing concentrations of carbonate in the sediment trap material at the central HAUSGARTEN site during and after the WWA are due to the strong increase in pteropod densities (Bauerfeind et al., 2014). The sudden mass occurrence of the sub-polar pteropod species *Limacina retroversa* reflects a northward displacement (range shift) of sub-arctic and temperate species. Still enhanced abundances of *L. retroversa* in years following the WWA (Busch et al., 2015) might point to an increased reproductive output of this originally sub-arctic species further south and a subsequent transport to the Fram Strait with the prevailing currents. A northward shift in the latitudinal distribution of boreal species was also found for other mesozooplankton organisms in the epipelagic zone of the West Spitsbergen Current (Weydmann et al., 2014). Between 2001 and 2009, Weydmann et al. (2014) observed a smooth change in dominance of ubiquitous and boreal/arctic taxa such as *Oithona similis* and *Triconia* sp. towards a stronger dominance of boreal taxa such as *Calanus finmarchicus*.

A similar range shift was found for pelagic amphipods, whereby the sub-arctic species *Themisto abyssorum* and the North Atlantic species *T. compressa* increasingly replaced the arctic species *T. libellula* during the WWA (Kraft et al., 2012). In fact, for Kongsfjorden (Svalbard), Hop et al. (2006) noticed the replacement of *T. libellula* by *T. abyssorum* already for the time period 1996-2002. Indicated by the presence of a complete temporal series of developmental stages, Kraft et al. (2013) found first evidence of reproductive success in the boreal amphipod species *T. compressa* at HAUSGARTEN observatory in 2011. Warm-water pulses in the WSC, like the WWA observed between 2005 and 2008, might also be

responsible for modern incursions of tropical Radiolaria into the Arctic Ocean, as detected by Bjørklund et al. (2012) in areas north of Svalbard.

Water temperature-related changes in the composition of the phyto- and zooplankton communities in the HAUSGARTEN area alter the flux of particulate matter to the seafloor with accompanying impacts on the entire food web and the marine biogeochemistry (Wohlers et al., 2009). Significantly increased concentrations in biogenic sediment components indicating the input of organic matter to the seafloor and the biomass of the small benthic biota during the WWA confirmed changes in the quantity and quality of the settling matter. Apparently, these changes directly impacted the entire benthic communities from bacteria to megafauna.

Changes in benthic bacterial communities along the bathymetric HAUSGARTEN transect off Svalbard were mostly driven by changes in the overall food availability (Jacob et al., 2013), whereas food quality is likely to affect the meiobenthic nematode communities. Although the trophic structure of the nematode communities is simple, and nematodes probably compete for the same bacterial-based food source, a similar amount of food of different quality may well have different effects on the community and could explain differences. According to Soetaert and Heip (1995), increased and high quality food supply could allow for a higher trophic complexity to develop within nematode communities. When the supply of organic matter to the bottom is high, a size-based food chain can develop within the nematode communities and predatory nematodes can become an important part of the food web (Soetaert and Heip, 1995). This might explain the comparably high proportions of predators/scavengers and omnivorous nematodes at the central HAUSGARTEN site in the years following the increased food availability in 2006/2007.

While time-series studies on bacterial and meiofauna (nematode) assemblages at the HAUSGARTEN observatory showed an immediate response to changes in food availability at the deep seafloor, megafaunal communities apparently reacted with some delay. In fact,

lowest megafaunal densities were found in 2007, when biogenic sediment compounds already indicated increased food availability at the deep seafloor. However, a 1-1.5-yr time lag in the response of the deep-sea megafauna to food availability, as observed by Ruhl (2007) for megafaunal assemblages in the deep North-East Pacific, could explain the significantly higher megafaunal densities in the eastern Fram Strait in 2011 and 2012. Interestingly, variations in megafaunal densities at HAUSGARTEN also coincided with significant changes in the trophic structure of the megafaunal community.

The major forcing on today's arctic environment is anthropogenic climate change, which is responsible for the recent increase in atmospheric and ocean temperatures over the Arctic (IPCC, 2013). However, even after 15 years of intense time-series work at HAUSGARTEN, we cannot yet judge with complete certainty whether the observed changes in environmental parameters and the marine biota indicate lasting alterations due to anthropologically-induced global changes, or whether they reflect natural variability on multiyear time-scales, for example, in relation to decadal oscillatory atmospheric processes expressed by indices such as the Atlantic Multidecadal Overturning (AMO), the North Atlantic Oscillation (NAO), and the Arctic Oscillation (AO) (e.g. Drinkwater et al., 2014).

Although we cannot conclude with absolute confidence that the WWA occurring in the Fram Strait between 2005 and 2008 is part of a broad human-induced shift towards a warmer Arctic Ocean, the observed alterations due to this warm water pulse may be seen as a "blueprint" for how the marine ecosystem might develop in an overall warming Arctic Ocean. However, apart from atmospheric and oceanic warming, the Arctic is also characterized by the presence of a number of other tipping elements (Duarte et al., 2012), including decreasing sea-ice coverage modifying heat fluxes and gas exchanges (Serreze et al., 2007), increased freshwater discharge from melting permafrost (Peterson et al., 2002), ocean acidification reducing CO_2 storage and calcification in organisms (Steinacher et al., 2009), and human

activities increasing the risk of pollution (Huntington et al., 2007; Bergmann and Klages, 2012; Obbard et al., 2014).

Long time-series studies remain the key tools to provide insights into processes and dynamics within an arctic marine ecosystem, and in fact, there is an urgent need for heightening efforts to study marine ecological variability and changes induced by climate change in the Arctic (Wassmann et al., 2011). Only long-term studies on seasonal to multi-decadal time scales will allow for improved predictions of the temporal development of the marine ecosystem in a future Arctic Ocean.

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